Bonn. zool. Beitr.	Bd. 47	H. 3—4	S. 301—311	Bonn, September 1998

The community of rock-dwelling cichlids in Lake Victoria

Ole Seehausen & Niels Bouton

Abstract. New data from southern Lake Victoria show that a large group of probably more than 200 species of stenotopic rock-dwelling cichlids remained unrecognized until recently, thus disproving prior assumptions about the eurytopic character of Lake Victoria cichlids. We discuss the ecology of rock-dwelling cichlids in Lake Victoria based on the community at an isolated rocky island in the Speke Gulf. With emphasis on micro-distribution and feeding ecology we present data on the faunistic and ecological composition of a typical community. Communities are rich in species and ecologically complex. This may make them particularly vulnerable to changes in the environment.

Key words. Cichlidae, Lake Victoria, community ecology.

Introduction

Species rich groups of stenotopic rock-dwelling cichlids made the cichlid species flocks of Lakes Malawi and Tanganyika world famous among fish ecologists, evolutionary biologists and aquarists (e.g. Fryer & Iles 1972, Lowe McConnell 1993). It is still widely believed that Lake Victoria cichlids are much less stenotopic and the coexistence of several hundred apparently eurytopic species was considered a violation of the competitive exclusion principle (Greenwood 1981). Though the existence of rock-dwelling cichlids in Lake Victoria was known (van Oijen et al. 1981), it was believed that there are only a handful of such stenotopic species. New research in southern Lake Victoria shows that a huge group of probably more than 200 species remained basically unrecognized. In many respects closely resembling the Mbuna of Lake Malawi, they prove much of the prior assumptions about the eurytopic character of Lake Victoria cichlids wrong. Most of them are restricted to rocky substrate, have a limited distribution within the lake and geographic variation is well developed. Unfortunately their communities are under severe pressure due to large scale changes in the environment. Several rock-restricted species have already disappeared (Witte et al. 1992) and, unlike in open waters, Nile perch predation is probably not the direct cause. An understanding of the complex ecological structure of the communities is a first step towards an understanding of these developments. We give here an introduction to the community ecology of rock-dwelling cichlids in Lake Victoria on the example of the community at an isolated rocky island in the Speke Gulf. We present data on the faunistic and ecological composition of a typical community with emphasis on micro-distribution and feeding ecology. We show the ecological complexity of the community and its species richness, qualities which may make it particularly vulnerable to alterations in the environment.

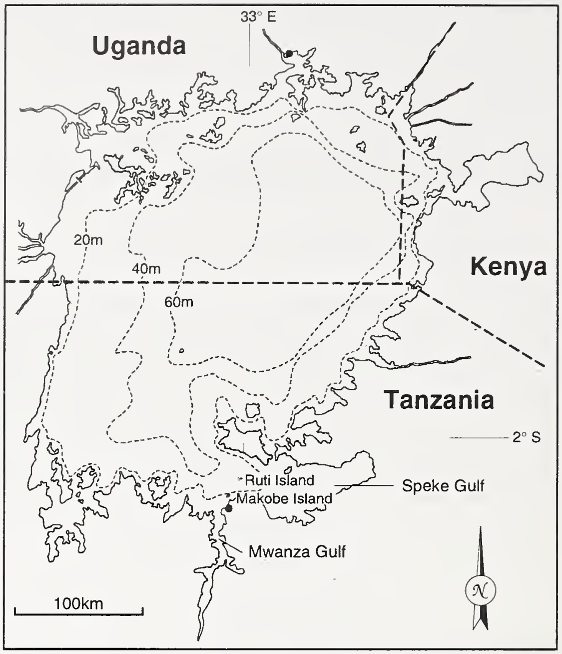

Fig. 1: Lake Victoria and the location of Makobe and Ruti Islands.

Materials and methods

Over a period of two and a half years (from January 1990 through July 1991, March to May 1992, September through December 1993 and February to April 1995) cichlids were sampled at the 0.075 km² (75 000 m²) small rocky Makobe Island which lies 5 km offshore in the Speke Gulf entrance (Fig. 1). Makobe Island is an example of gently sloping islands with small to medium sized rock boulders and moderate geographical isolation. Sampling was done from the surface down to 6 m depth with gillnets of mesh sizes between 1 and 2 inches and by angling in rock pools and rocky crevices. The total sampling effort consisted of over 48 000 m² net hours and over 300 hours angling. Additionally underwater censuses were done by snorkeling. Relative abundances were determined with all three techniques. Microhabitat distribution of the species was scored by restricting samples to areas of one to a few square meters of rather uniform depth, exposure and rock cover.

Stomach contents of some individuals of each species were analyzed individually to identify food organisms. The contents of 40 individuals per species (each 10 from four seasons) were then centrifuged and quantified. It is necessary to study not only diet composition and spatial distribution but also how the food is obtained. We performed feeding experiments in the laboratory with the very species whose diet was analyzed. We studied the behaviour of fish feeding in experimental aquaria on *Aufwuchs* (algae and associated fauna) covered rocks from their natural habitat. After collection from the lake the fish were kept in aquaria without food for 40—48 hours and were then offered *Aufwuchs*-covered stones from the lake. Feeding behaviour was scored over a period of 30 minutes with two or three individuals per experiment. Experiments were done for 9 to 15 individuals per species. To get a broader impression of the feeding repertoires that rock frequenting Lake Victoria haplochromines possess, the feeding behaviour of a few individuals of some less abundant species was studied as well. We calculated diet-overlap and behaviour overlap as the sum of the overlap per food item or feeding technique respectively.

With three exceptions (*Neochromis nigricans, "H." nyererei, Paralabidochromis chilotes*) the species used for this study are not formally described. Preliminary diagnoses and colour photographs were published recently (Seehausen 1996). A number of papers on their ecology, eco-morphology and taxonomy have been published (Seehausen & Bouton 1997; Bouton, Seehausen & van Alphen in press; Seehausen, Bouton, Zwennes & Lippitsch in prep.). In the meantime we use cheironyms for the undescribed species. Species recognition criteria used are those outlined by Seehausen (1996).

With regard to the generic taxonomy of Lake Victoria cichlids considerable heterogeneity is prevalent in recent publications with some authors following Greenwood's last general revision of 1980, others not. Though some of Greenwood's genera, we believe, need to be redefined, we could assign many of the new species. For those that we could not assign, we use the old generic name "*Haplochromis*" in quotation marks.

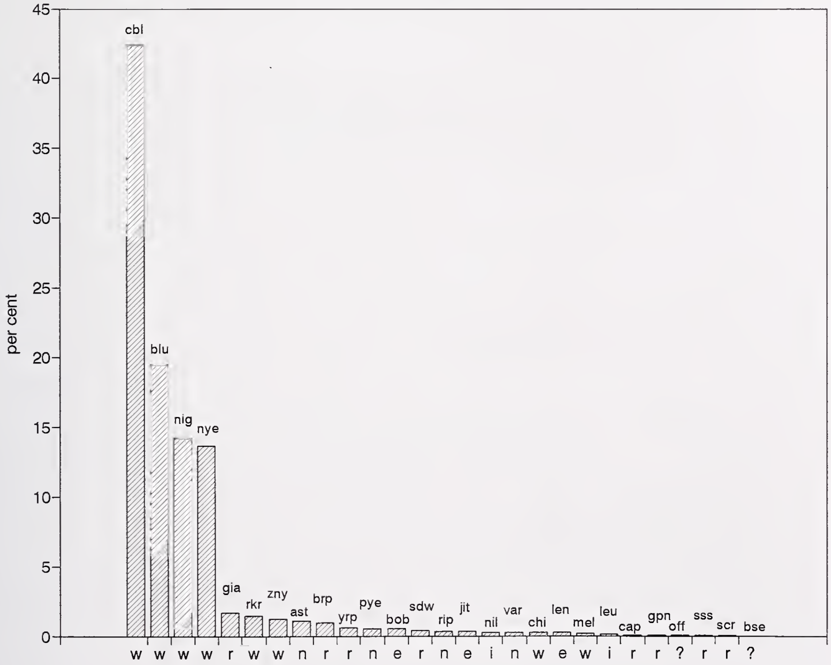

Fig. 2: Species abundance distribution at Makobe Island. Means of four sampling periods (n = 5919 fishes): abbreviations as in table 1. n = widely distributed, non-rock-restricted species, w = widely distributed rock-restricted species, r = regional rock-restricted species, e = local endemics, i = introduced species, non-rock-restricted.

Table 1: List of cichlid species occurring at Makobe Island/Speke Gulf. ++++ widely distributed, non-rock-restricted spp., +++ widely distributed rock-restricted spp., ++ regional rock-restricted spp., + local endemics, x introduced species, non-rock-restricted.

Algae scrapers	
Haplochromis "purple yellow"	++++
Neochromis nigricans (NIG)	+++
Neochromis "giant scraper" (GIA)	++
Neochromis "blue scraper" (BLU)	+++
Xystichromis "carp" (CAP)	++
Paralabidochromis "short snout scraper" (SSS)	++
Neochromis "large eye nigricans" (LEN)	+
Xystichromis "jitu" (JIT)	+
Haplochromis "blue obliquidens" (BOB)	+
Algae scrapers / Detritus eaters	
Oreochromis variabilis (VAR)	++++
Xystichromis "copper black" (CBL)	+++
Oreochromis niloticus (NIL)	x
Oreochromis leucostictus (LEU)	x
Animal *Aufwuchs* eaters	
Psammochromis riponianus (RIP)	++++
Paralabidochromis "rockkribensis" (RKR)	+++
Paralabidochromis chilotes (CHI)	+++
"*H.*" "zebra nyererei" (ZNY)	+++
Paralabidochromis "blue rockpicker" (BRP)	++
Paralabidochromis "yellow pseudorockpicker" (YRP)	++
"*H.*" "yellow chin pseudonigricans" (GPN)	++
"*H.*" "pink anal" (SDW)	++
Plankton eaters	
"*H.*" *nyererei* (NYE)	+++
Mollusc eaters	
Astatoreochromis alluaudi (AST)	++++
"*H.*" "striped crusher" (SCR)	++
Paedophages	
Lipochromis cf. *melanopterus* (MEL)	+++
food unknown	
"*H.*" "offshore" (OFF)	?
"*H.*" "blue secret" (BSE)	?

Results

I. Faunal composition and abundance distribution

The community at Makobe Island is composed of at least twenty-seven cichlid species (table 1). They can be assigned to five groups of different gross distribution patterns: 15 % are species widely distributed in Lake Victoria and not restricted to rocky substrates. All others are restricted to rocky substrates though they may occur in the immediate vicinity of rocks above other substrata. 30 % are species widely distributed at rocky shores and islands, 30 % are species with regionally restricted distribution (i.e. western Speke Gulf species), 11 % are endemics of Makobe Island and 7 % are introduced species (*Oreochromis niloticus* and *O. leucostictus*). The distribution of two species is not known. Figure 2 gives the mean abundance distribution at Makobe Island obtained over four sampling periods (n = 5919 fishes) and relates relative abundances to the distribution pattern groups. It shows that most of the numerically dominant species are species with a wide distribution, while most regional and all local endemics occur in low densities. This pattern was rather stable over the sampling years. Very similar results were obtained at another island in the Speke Gulf, Ruti Island, which is a steeply sloping island with very large compact rock boulders. This indicates (and is confirmed by samples from many other places), that the species that numerically dominate at one place do so at most of the places where they occur.

II. Spatial community structure

Figure 3 shows the relative abundance of the four dominant and some other species in different microhabitats and depths. Figure 3a is based on angling and net samples, Figure 3b on underwater censuses. The species show significantly different vertical distributions (Fisher's exact probability test $p < 0.05$). Figure 4 gives two examples of horizontal species distribution patterns indicating that horizontal patterns are species specific as well. They reflect not only differences in microhabitat requirements but likely also different degrees of microhabitat stenotopy. *Xystichromis* "copper black" lives in a wide range of microhabitats from the surf zone to several meters depth, between rocks of all boulder sizes and at strongly surf exposed places as well as in protected embayments and under floating vegetation. This relatively wide ecological range enables the species to inhabit a large part of the available rocky habitat. Its distribution is not indicated in Figure 4 because it was found in each of the 10 x 10 m squares. Widely distributed in the offshore waters but largely absent from the inshore areas is "*H*." *nyererei* (Fig. 4) while "*H*." "zebra nyererei" is restricted to crevices between medium sized rocks along the shore and at rocky islets. *Haplochromis* "blue obliquidens" finally, as an extreme example, occurs exclusively in less than 2 m depth on the surface of gently sloping rock fields in surf protected embayments (Fig. 4). It appears that more or less specific demands restrict the distribution of species to differently sized fractions of the potentially available rocky habitat. However, it is not yet understood whether interspecific competition plays a role in delimiting the microhabitat distribution of some species.

III. Trophic community structure

Figure 5a shows the result of laboratory feeding experiments for the four most abundant species plus two rare species. Feeding techniques are defined elsewhere (Seehausen, Bouton, van Alphen, Witte submitted). The composition of feeding ethograms of the six species differs quantitatively significantly different (U-test $p<0.05$). Coefficients for overlap are given in table 2. The species can be assigned to three major feeding behaviour groups according to the predominantly employed feeding technique: pull-scrapers, pickers (both benthic foragers) and snappers (pelagic foragers). Since behavioural differences were recorded in the absence of interspecific competition they are to be considered autecological.

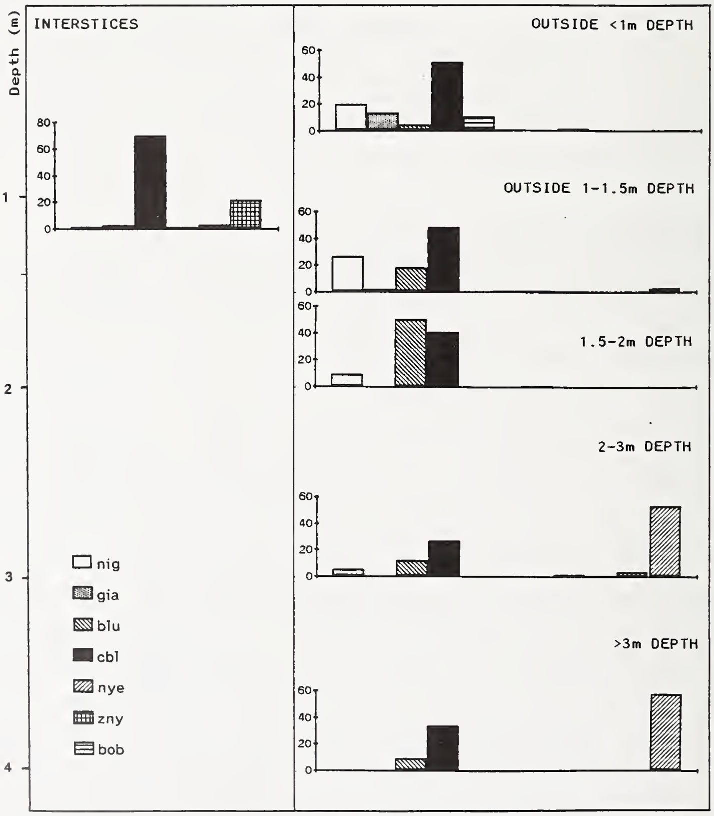

Fig. 3a: Examples of vertical habitat segregation. Relative densities of rock-dwelling haplochromine species in different microhabitats at Makobe Island: Interstices between rocks in shallow water and different depth ranges outside of the interstices. Based on net and angling samples. Abbreviations as in table 1.

Figure 5b shows the result of stomach content analyses for the same species. The four abundant species disperse over three major trophic groups that correspond to the three feeding behaviour groups: scrapers of filamentous algae, loose algae/ animal *Aufwuchs* eaters, and plankton eaters. A fourth trophic group, not reflected in the feeding behaviour due to absence of its specific prey, are snail eaters. However, their specific feeding technique, pharyngeal crushing, is well known (Greenwood 1974). The interspecific differences in diet are significant (U test $p<0.05$) with the exception of that between the two algae scrapers *N. nigricans* and *N.* "blue scraper". Coefficients for diet-overlap are given in table 2.

Several other trophic groups are rather consistent members of rock cichlid communities: pedophages, piscivores and crab eaters. These larger predators probably always occurred in lower densities than *Aufwuchs* and plankton feeders, however, after the Nile perch upsurge they completely disappeared at many places. At Makobe Island we frequently caught one pedophagous species (Table 1).

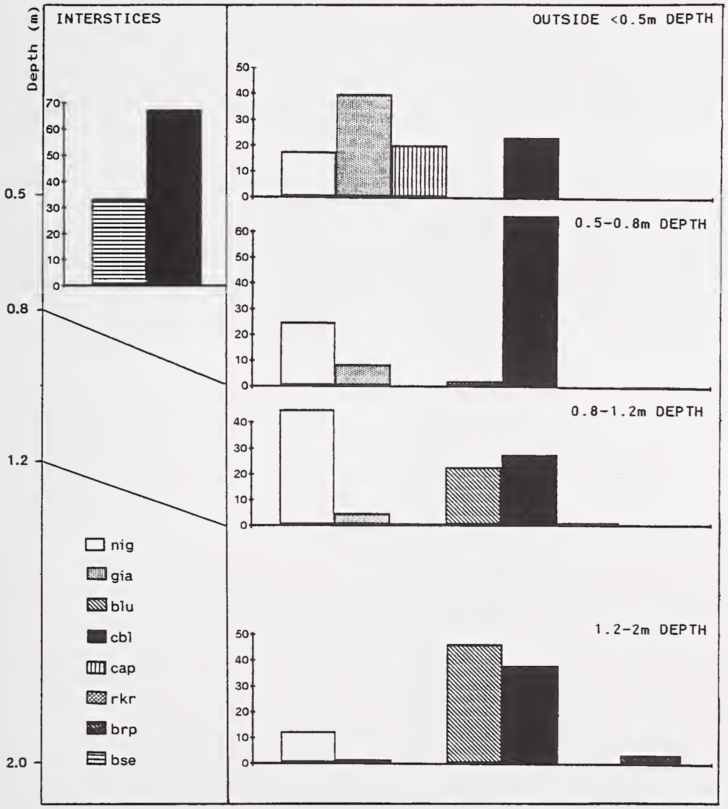

Fig. 3b: Same as 3a but based on underwater censuses.

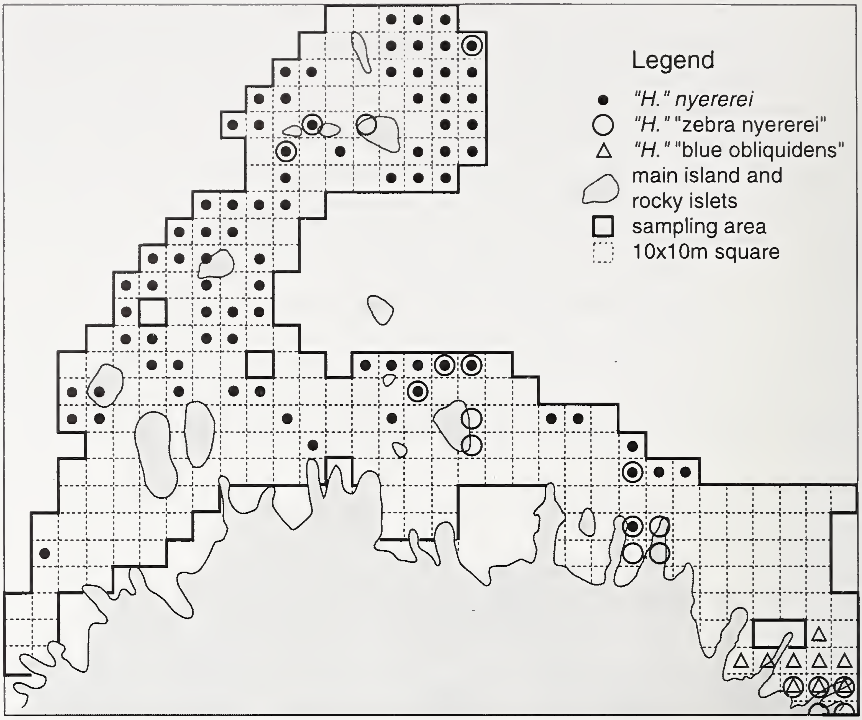

Fig. 4: Examples of horizontal habitat segregation among haplochromine species at the west shore of Makobe Island. Among a pair of sibling species "H." "zebra nyererei" lives more inshore and in the immediate vicinity of rocky outcrops than "H." *nyererei*. Only the first one occurs frequently in crevices and rockpools within the island in several metres distance from the lake. *H.* "blue obliquidens" occurs only at small patches of suitable microhabitat.

Table 2: Coefficients of trophic niche overlap.

Diet						Feeding behaviour					
	NIG	BLU	CBL	ZNY	NYE		NIG	BLU	CBL	ZNY	NYE
BLU	.90					BLU	.85				
CBL	.59	.57				CBL	.47	.56			
ZNY	.29	.31	.31			ZNY	.36	.45	.88		
NYE	.12	.12	.12	.70		NYE	.44	.52	.61	.73	
AST	.00	.00	.00	.00	.00	AST	.22	.25	.49	.66	.39

Discussion

The studied community of rock-dwelling cichlids in Lake Victoria shows a rich ecological structure. It is characterized by few very abundant and many rare species. The abundant species are usually widely distributed and represent the three trophic groups that at many places allow the highest levels of population density: scrapers

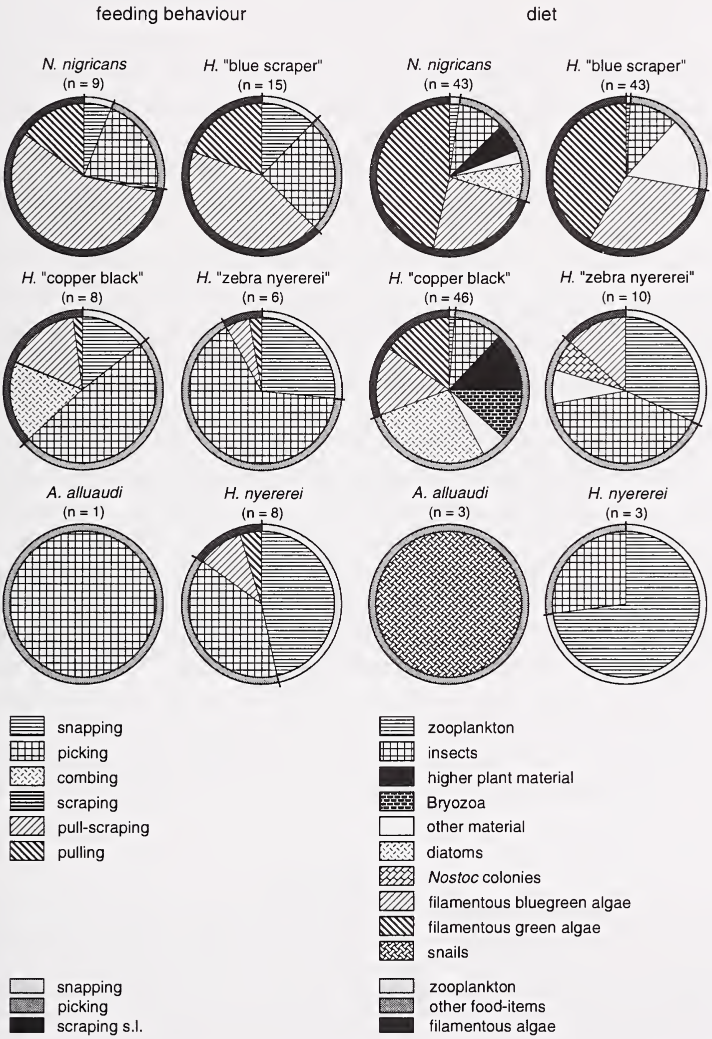

Fig. 5: Left two columns: feeding behaviour ethograms of the four numerically dominant and two other species at Makobe Island. Right two columns: Composition of the diet of the four numerically dominant and two other species at Makobe Island. In the outer circle several categories are lumped to form three principal feeding techniques and the three major food categories that reflect them.

of filamentous algae, loose algae/animal *Aufwuchs* eaters and planktivores. Most locally endemic species occur in low densities. This pattern may suggest that the key niches in the communities of rocky habitat islands were filled by a few species early during the formation of the present days lake and that the finer ecological community structure is largely a secondary phenomenon due to ecological differentiation and speciation that happened on regional scales. This is a hypothesis that calls for tests by interdisciplinary approaches.

The different species in the rock cichlid community can be well characterized ecologically. Each occupies only a particular portion of the total ecological niche available to rock-dwelling cichlids. The differences, however, are subtle and the ecological packing is very dense. Only the upper five meters are occupied by epilithic *Aufwuchs* scrapers but ten such species share this narrow depth zone. The peaks of their relative abundance are in different microhabitats and depths but those of neighbouring species are separated by no more than one to two meters. Among them are three of the four numerically dominant species. Trophic morphology of two of them (*N. nigricans, N.* "blue scraper") is so similar that it is difficult to identify preserved specimens that lost colouration. Yet they exhibit autecological differences in feeding behaviour which, together with subtle aut- or synecological differences in microhabitat distribution (and possibly synecological competition effects on feeding behaviour), result in significantly reduced diet overlap.

There is no evidence that the cichlid species assemblage of Makobe Island violates the competitive exclusion principle but the dense spatial packing of morphologically and ecologically very similar species is likely to make the community highly susceptable to changes in the environment. Tightening and relaxation of interspecific competition may under such circumstances be some immediate response to contraction and expansion of the habitat. Some fluctuation of habitat width is a natural seasonal phenomenon caused by water level fluctuations. However, recently more dramatic changes take place that lead to a more permanent alteration of the habitat: water transparencies are significantly decreasing since at least the late seventies, reducing the habitat width for algae feeders, and upwelling of anoxic waters at steep rocky cliffs affects the communities of planktivores and benthivores in deeper waters. It is possible that such processes add to the species loss in rocky areas that is caused by the impact of turbidity on colour vision and species-assortative mating (Seehausen, van Alphen & Witte 1997) but much more work is needed to understand this.

Acknowledgements

Many thanks to Jacques van Alphen, Kees Barel and Frans Witte for their critical advice on the manuscript. We are indebted to Mhoja Kayeba, Ruben Enoka, Anna Samwel Terry, Masoud Ilomo, Ali Marwa and Aloys Peter for their expertise in the fieldwork. Radhmina and Gonza Mbilinyi are thanked for much logistic support. The Tanzania Fisheries Research Institute (TAFIRI) and its director Prof. P.O.J. Bwathondi are thanked for the research permit. The director of the Mwanza centre of TAFIRI, Mr. Egid F.B. Katunzi and our colleagues at the centre are thanked for hospitality and support during our stays. The Nyegezi Freshwater Fisheries Research Institute and its Principal Mr. R. R. Mapunda are thanked for logistical help and Martin Brittijn for drawing some of the figures. This study was made possible due to WOTRO grant no. W84-282 and, thanks to the effort of L. Schadhauser from "Wild about animals" magazine, was subsidized by the TETRA Company in 1993.

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Zeitschrift/Journal: Bonn zoological Bulletin - früher Bonner Zoologische Beiträge.

Jahr/Year: 1997/1998

Band/Volume: 47

Autor(en)/Author(s): Seehausen Ole, Bouton Niels

Artikel/Article: The community of rock-dwelling cichlids in Lake Victoria 301-311